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Ecological Responses of *Osmunda regalis* to Forest Canopy Cover and Grazing

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Abstract.—The density and frond traits of the dimorphic fern *Osmunda regalis* were examined in 45 populations situated in central Italy, along a gradient of forest canopy cover and deer grazing. The survey involved 1704 ramets containing 6416 fronds, of which 5643 were sterile and 773 fertile. Within the ramets, the number of fertile fronds increased with the number of sterile fronds and with the mean height of ramets. Light seemed to promote fertility, as the number of fertile fronds decreased with increasing canopy cover. Fewer and smaller fronds were found in plots with high forest canopy cover. Our results showed that *O. regalis* performed best in conditions of full sunlight but can persist and recruit young sporophytes under closed canopy. As many marsh and lake environments have disappeared or been altered by human activity, more populations were located under high canopy cover in the forest than in open habitats. Deer grazing caused a significant decrease in fertile fronds, in total frond area and in ramet height, but the number of ramets and sterile fronds were unaffected. In conclusion, plant density and frond traits of *O. regalis* responded differently to the availability of light and to grazing.

Key Words.—deer, fertile fronds, fern, Italy, populations, ramets, sporophyte, sterile fronds

Research on the effects of light on the density and frond traits of fern sporophytes can reveal important aspects of fern ecology and their role in forests, and may be a useful means of protecting endangered species. According to a recent critical review (Mehltreter, 2008), few researchers have contributed to this branch of ecological studies and the results are consequently restricted to a limited number of sites, which are usually located in the tropics as the majority of ferns are found there. Moreover, while many investigations have been carried out on tree-like ferns or tree ferns, especially due to commercial interest in many of them (i.e., Williams-Linera, 1997; Arens and Sánchez-Baracaldo, 2000; Arens, 2001; Chiou *et al.*, 2001; Mehltreter and García-Franco, 2008; Eleutério, 2009), few studies have examined herbaceous ferns.

An overview of research concerning the effect of light availability on the density and frond traits of herbaceous ferns showed that: frond density in *Dennstaedtia punctilobula* (Michx.) Moore increases with the intensity of light (Hammen, 1993); the sporophylls of *Matteuccia struthiopteris* (L.) Tod. increase with increased sunlight (Prange and von Aderkas; 1985, Odland *et al.*, 2006); the specific leaf area of various *Blechnum* species decreases with the increasing availability of light (Saldaña *et al.*, 2005); the rate of leaf

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development to maturity in *Rumohra adiantiformis* (Forst.) Ching is strongly related to solar radiation (Strandberg, 2003); stem growth rates and the percentage of stems with sori in *Oleandra pistillaris* (Sw.) C. Chr. were higher in the open than in the understorey (Takahashi and Mikami, 2006). Furthermore, research by Kluthe (2006) underlined that some selected fern species (*Athyrium filix-femina* "Frizelliae", *A. niponicum* "Pictum", *Dryopteris celsa* (W. Palmer) Knowlt., *D. erythrosora* (D.C. Eaton) O. Kuntze and *Matteuccia struthiopteris*) were significantly larger in 80% shade treatments than in 50% shade treatments, in relation to one or more of the parameters measured (total area, length or width of fronds).

It has been observed that the utilization of leaf primordia in *Osmunda cinnamomea* L. increased considerably following the removal of canopy and the consequent increase in light intensity (Jordan and Kuehnert, 1975). Nevertheless, light availability can have limited impact on the distribution, abundance and morphological parameters of other fern species (see Hill and Silander, 2001; Kluthe, 2006). Studies on the developmental stages of sporophytes have shown that light intensity may have different effects on mature and sporeling stages within the same species (Cinquemani Kuehn and Leopold, 1993). Other studies have shown correlations between frond size, growth and fertility and various environmental factors (i.e., temperature, water characteristics, etc.) (Odland, 1995; Vöge, 1997a; Vöge, 1997b; Odland, 1998; Odland et al., 2004).

Research into the effects of deer grazing on fern density and frond traits is scarce. Unlike spermatophytes, pteridophytes are less favored by and often unpalatable to deer (Nugent, 1990; Kraus, 1992; Suzuki *et al.*, 2008). However, studies carried out at the species level have pointed out that deer include some ferns among the favorite plants in their diet (see Forsyth *et al.*, 2002; 2005). This preference may be a result of seasonal variation, as ferns are important in the diet during late autumn, winter and early spring when they are one of the few sources of green leaves (Healy, 1971).

The goal of this study was to analyze whether and how a forest canopy cover gradient and deer grazing affect density and frond traits in some natural populations of royal fern (*Osmunda regalis* L. subsp. *regalis*). Analyses were performed at ramet level to investigate the relationship between traits, and at plot level to test the effect of canopy cover and grazing.

Osmunda regalis is a deciduous herbaceous fern with sterile fronds (trophophylls) and fertile fronds (trophosphorophylls), the latter bearing sporangia at their apex. The research was conducted in Tuscany (central Italy) where the species occurrence is mainly restricted to small, undisturbed habitat patches that offer the most favorable environmental conditions (see Landi and Angiolini, 2008). The worldwide distribution of *O. regalis* is connected to areas with sub-oceanic climates and the species has not adapted to either continental or dry climates (Pichi Sermolli, 1970; 1979). For this reason it is common in western Europe, where the Mediterranean regions (i.e., Spain and Italy) represent the southern limit of its distribution (Jalas and Suominen, 1972). In Italy the species is only present along the Alpine arc and in the

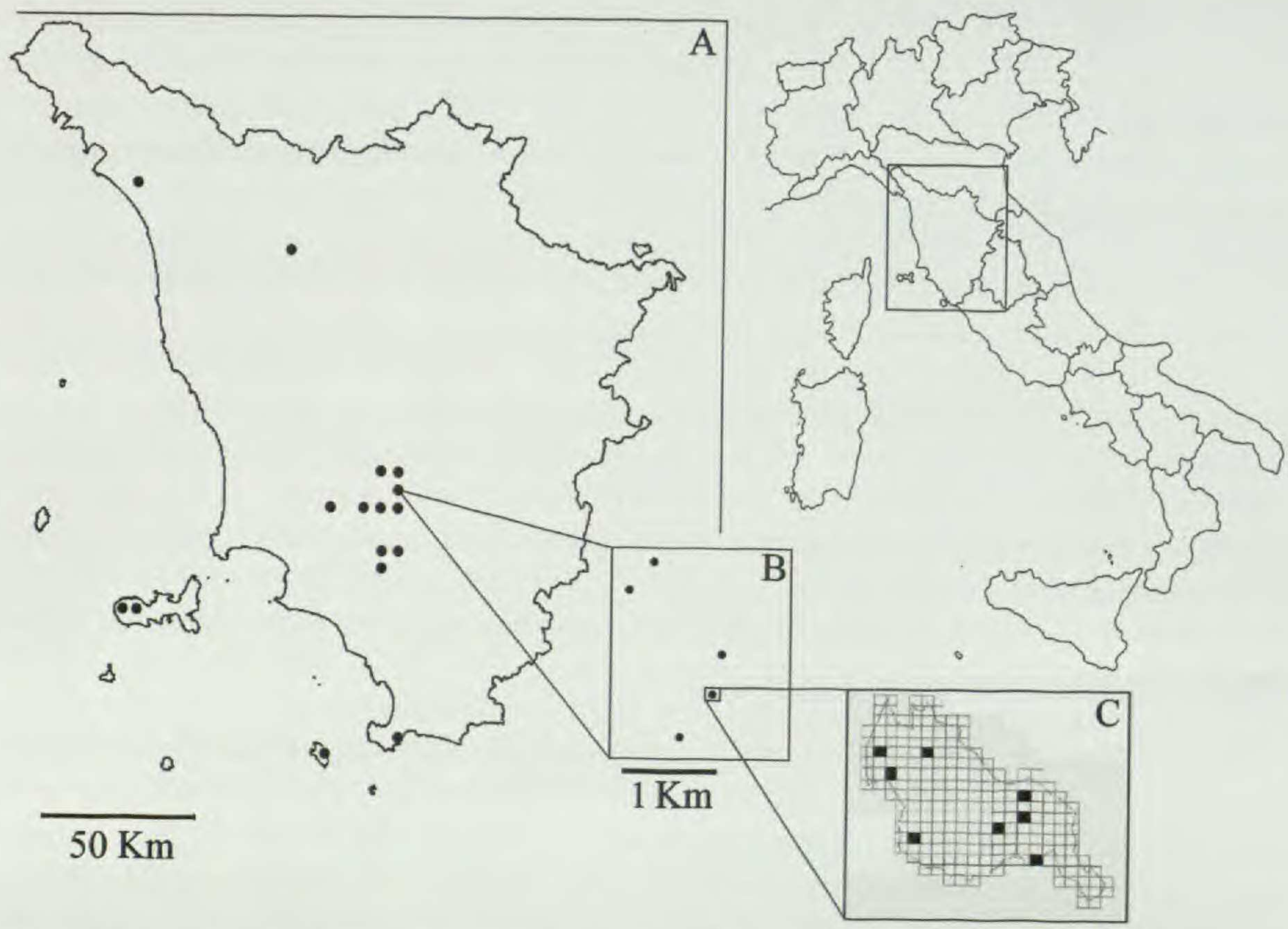

FIG. 1. Location map of the study area and sites investigated, showing dots representing 5 × 5 km grids (A), an example of the population distribution (B), and a representation of the random sampling design in a population (C); the black filled squares of 5 × 5 m indicate the plot sampled.

Tyrrhenian regions (Bizzarri, 1963; Marchetti, 2003) where it is often considered rare (see Camoletto Pasin *et al.*, 2000; Landi and Angiolini, 2007). The rarity of *O. regalis* in Tuscany is related not only to its geographically marginal position but also to the reduction or alteration (reclamation and water catchment) of the habitats in which it grows (Landi and Angiolini, 2007). The royal fern is also catalogued as rare and threatened in some regions of Spain where it is employed for medicinal uses and its harvesting is not strictly regulated (Molina *et al.*, 2009), and has decreased significantly in many other countries of Europe (Tutin *et al.*, 1993).

Materials and Methods

The study was conducted between June and August 2006 on 45 natural populations of *Osmunda regalis* (*Osmundaceae*) located in Tuscany (central Italy, Fig. 1), at an altitude ranging between 5 and 620 m a.s.l.. Many of the larger populations occur at altitudes between 300 and 400m and with northeastern exposure (Landi and Angiolini, 2008). The majority of known *O. regalis* sites were investigated in this study, in order to cover all habitat types. The habitats occupied by these populations are swamps developing at or along the outflow of springs, the edge of streams and small marshes. The region investigated is characterized by a Mediterranean climate. According to the meteorological stations (15 stations) closest to the populations, the mean annual precipitation is 916 mm/yr (±211 S.D.) and the mean annual temperature is 14.7 °C (±1.3 S.D.). The vegetation surrounding the populations is mainly composed of deciduous forests (Landi and Angiolini, 2010), and the tree species found in the fern populations (from most to least frequent, with the exception of rare species) are: *Fraxinus ornus* L., *Alnus glutinosa* (L.) Gaertn., *Castanea sativa* Mill., *Ilex aquifolium* L., *Quercus ilex* L., *Sorbus torminalis* (L.) Crantz, *Frangula alnus* Mill., *Arbutus unedo* L., *Carpinus betulus* L. and *Populus tremula* L.. The substrate of the sites is quite homogeneous and includes metamorphic units, magmatic rocks and quaternary deposits, with generally acidic or subacidic reaction. The only deer species present are fallow deer (*Dama dama* Linnaeus, 1758) and roe deer (*Capreolus capreolus* Linnaeus, 1758). A 2006 census by the Faunal Resources and Nature Reserve Service of the Province of Siena revealed that the deer density in the Merse Valley area, where *O. regalis* is most abundant (see Landi and Angiolini, 2008), is estimated at 12 animals/100 ha.

The *O. regalis* populations were defined as discrete clusters of plants, separated from other clusters by at least 500 m (Fig. 1b). Each population area was defined as a regular-shaped polygon covering the bulk of the population and 5 m × 5 m plots were randomly selected on a grid in order to sample 5% of the population (Fig 1c). Then, in order to obtain a representative sample of each population, a number of plots was selected in proportion to the surface area occupied by each population. For each ramet (a ramet being one but usually more fronds growing out of the rootstock like a crown, see Kenkel, 1996; Landi and Angiolini, 2008) the following attributes were recorded: number of fertile and sterile fronds, height, size of the fronds expressed as area (length × mean width) and presence of grazing damage on each frond. For each of 128 plots investigated the following parameters were counted or measured: number of ramets, number of fertile and sterile fronds, mean height of ramets and total frond area (sum of the frond size).

We also measured forest canopy cover by ocular estimation (as a percentage) at the center of the plot. Canopy cover is defined as the proportion of the forest floor covered by the vertical projection of the tree crowns (Jennings *et al.*, 1999), including foliage and plant material from species rooted both within and outside the plot.

At the ramet level, a one-way ANOVA was applied in order to determine the differences in the number of fertile fronds (response variable) between ramets with different numbers of sterile fronds (categorical predictor). In order to estimate the differences between the means, the Tukey HSD post-hoc multiple comparison test for unequal samples was applied, with a significance level of 0.05. At the plot level, regression analysis was used to investigate the responses of density and frond traits (dependent variables) to the forest canopy cover gradient (independent variable), and the correlations between dependent variables were identified by a correlation matrix. All the above analyses were only performed in plots containing ramets without damage due to

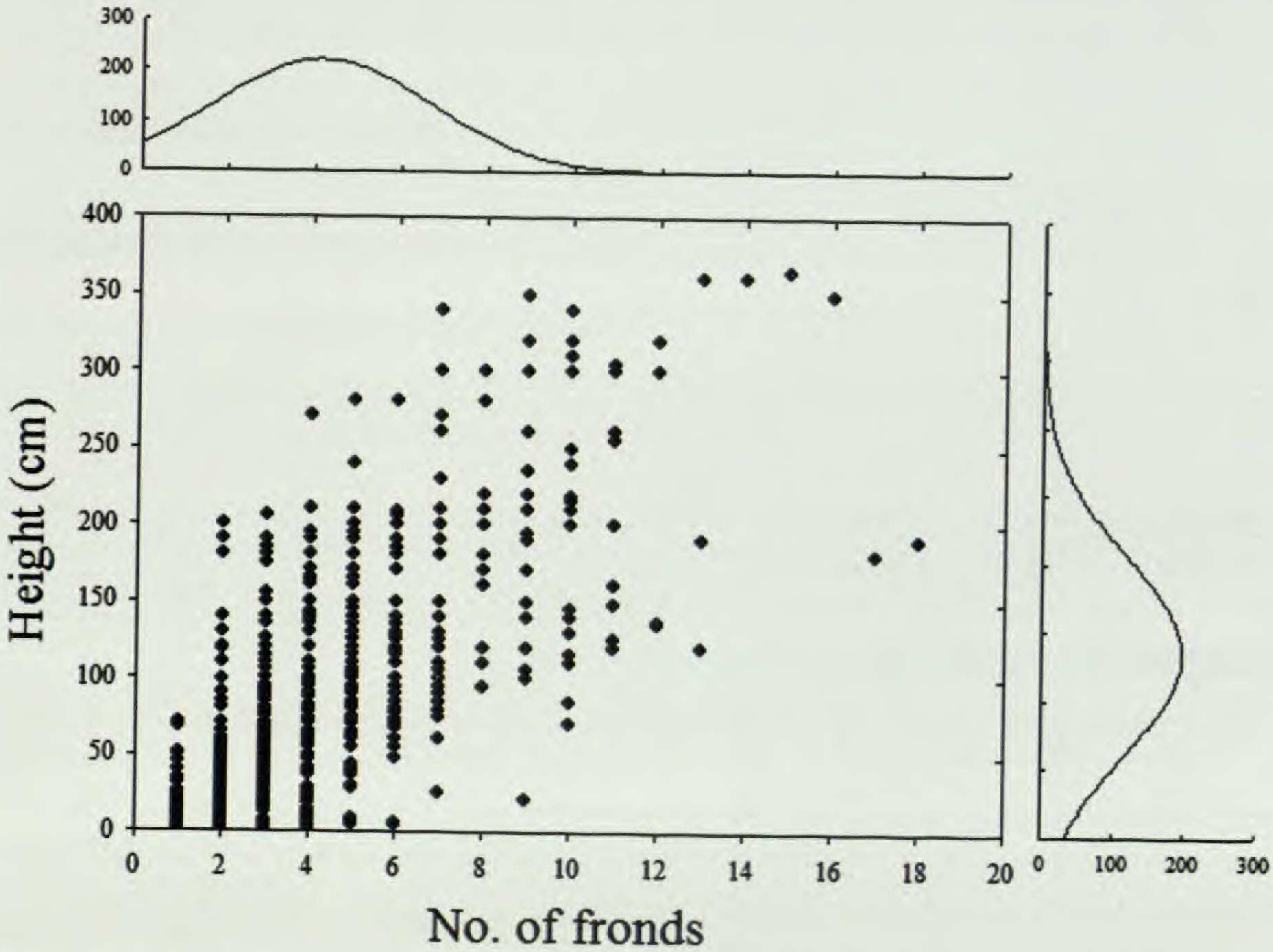

FIG. 2. Relationship between total number of fronds (sterile and fertile) and height of ramets (no. = 876). The frequency distribution of ramets is shown alongside the axes.

grazing. Ramets and fronds with mechanical breakages were excluded from all analyses. A two-way ANOVA was used to test the effects of canopy cover (divided into open and forest), grazing (divided into grazed and ungrazed), and their interaction on frond traits (dependent variables) such as the number of ramets, number of fertile and sterile fronds, total frond area and mean height per plot. In this analysis, the open category included plots with canopy cover between 0 and 50% and the forest category included plots with canopy cover between 51 and 100%. The statistical analyses were performed using STATISTICA (StatSoft Inc., 2005).

RESULTS

Density and frond traits.—A total of 1704 ramets containing 6416 fronds were investigated, of which 5643 were sterile and 773 fertile. There were 876 ungrazed ramets with 3612 fronds, of which 586 (19.4%) were fertile.

The increase in the height of ramets was correlated with an increase in the number of fronds (Fig. 2). Most of the ramets consisted of 3–5 fronds and had a height of between 100 and 150 cm. One ramet had 18 fronds and the largest ramet reached a maximum height of 365 cm.

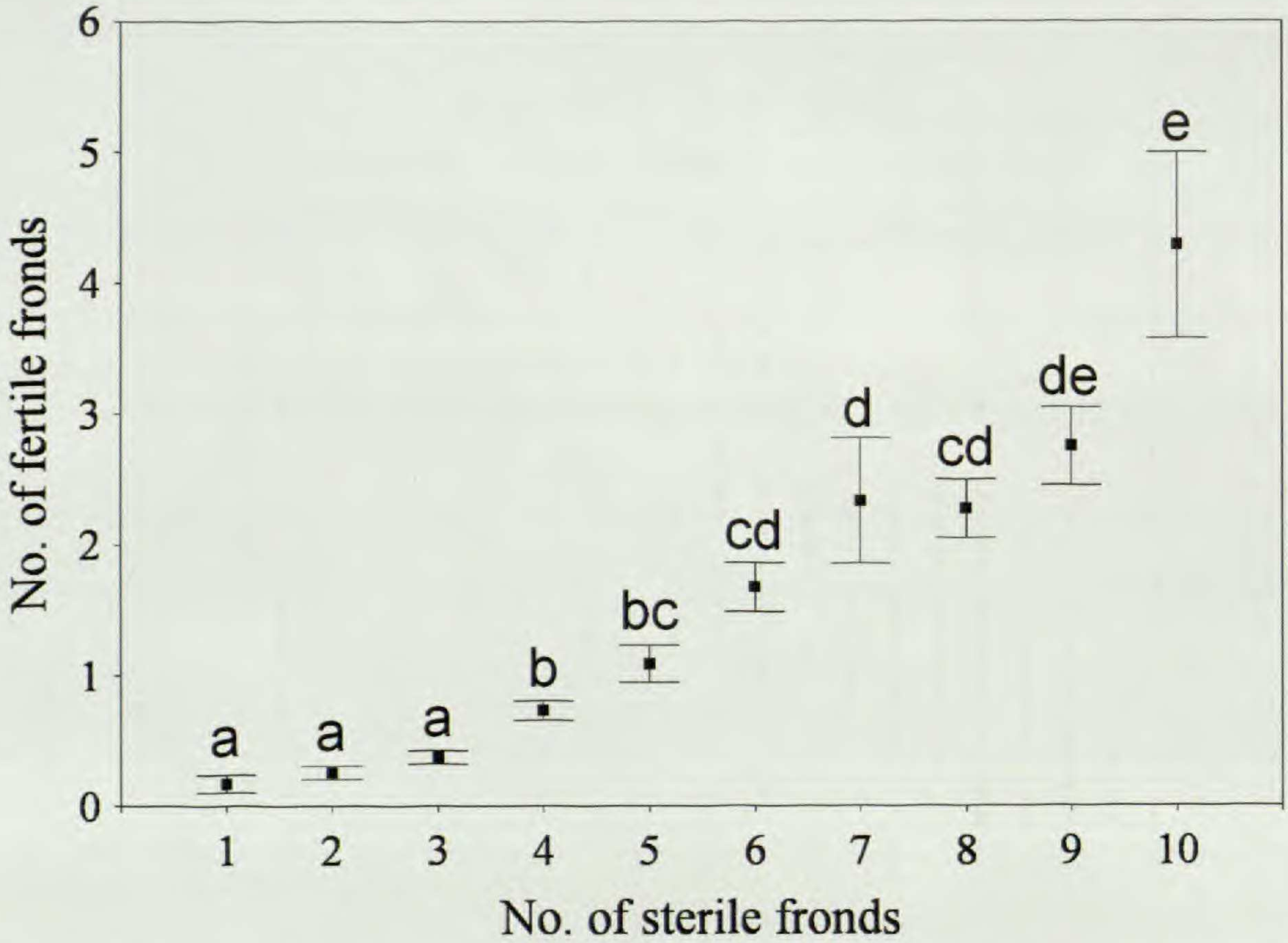

FIG. 3. Differences in number of fertile fronds between ramets (n = 876) with different numbers of sterile fronds. Symbols represent the mean (dark squares) and standard error (vertical bars). Different letters indicate significant differences according to Tukey's test for unequal samples at the $P < 0.05$ level.

There were significant differences in the number of fertile fronds between groups of ramets with different numbers of sterile fronds (one-way ANOVA, $F_{9,866} = 36.73$, $P < 0.01$). However, the number of fertile fronds also varied between groups of ramets and Tukey's test showed significant differences between groups with more than three sterile fronds (Fig. 3).

The number of fertile and sterile fronds, total frond area and mean height of ramets were all positively and significantly correlated (Table 1). However, while the mean height of ramets was strongly correlated with the number of fertile fronds and total frond area, it was weakly correlated with number of

TABLE 1. Matrix of correlation coefficients between density and frond traits sampled at plot level (no. = 78). * indicates significance at the 0.01 level.

	Ramets (no.)	Fertile fronds	Sterile fronds	Total frond area
Fertile fronds (no.)	0.282			
Sterile fronds (no.)	0.905*	0.547*		
Total frond area (m^2)	0.417*	0.785*	0.666*	
Mean height of the ramets (cm)	0.083	0.791*	0.379*	0.831*

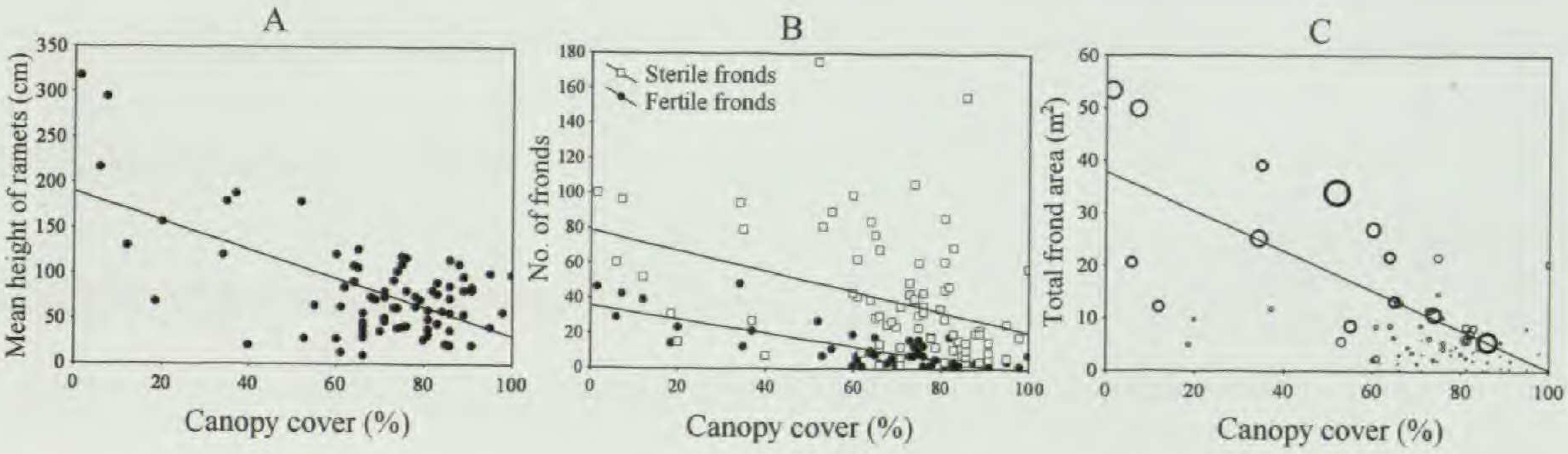

FIG. 4. The relationship between percent forest canopy cover and mean height of ramets (A), number of sterile fronds (white squares) and fertile fronds (black dots) (B), and total frond area, with circle sizes proportional to the number of fronds (C) which ranged from 1 to 202 (mean = 46.3 ± 41.9 SD). All data were collected in ungrazed plots (no. = 78).

sterile fronds. The density of ramets (no. of ramets/plot) showed no significant correlation with mean height or the number of fertile fronds.

Response to forest canopy cover gradient.—Forest canopy cover ranged from 1–100%, but most plots (57 out of 78 the ungrazed plots) had over 60% cover. The mean height of ramets (R^2 = 0.382, P < 0.01; Fig. 4a) and number of fertile fronds (R^2 = 0.614; P < 0.01; black dots in Fig. 4b) responded negatively to increasing canopy cover. Canopy cover had a weak influence on the number of sterile fronds (R^2 = 0.131; P < 0.01; white squares in Fig. 4b), but was negatively correlated with the total frond area (R^2 = 0.363; P < 0.01) and the number of fronds (R^2 = 0.476; P < 0.01; Fig. 4c). The relationship between the number of ramets and forest canopy cover gradient was not significant.

Effect of deer grazing and interaction between grazing and canopy cover.—Fronds grazed by deer were detected in 50 plots belonging to 21 populations, while the fronds in the 78 ungrazed plots belonged to 38 populations; in 12 populations both types of plot (grazed and ungrazed) were detected. Two-way ANOVA revealed significant effects of grazing on the number of fertile fronds ($F_{1,124}$ = 26.01; P < 0.01), mean height ($F_{1,124}$ = 18.88; P < 0.01) and total frond area ($F_{1,124}$ = 10.64; P < 0.01). In the grazed plots these frond traits were lower than in ungrazed plots (their mean values decreased by approximately 50%, 30% and 26% respectively, see Table. 2). In addition, interaction between canopy cover and grazing significantly affected the number of fertile fronds ($F_{1,124}$ = 19.20; P < 0.01), mean height ($F_{1,124}$ = 10.18; P < 0.01) and total frond

TABLE 2. Mean ± SD of number of *O. regalis* ramets and frond traits in all plots, in ungrazed plots and in plots grazed by deer.

	All plots (128)	Ungrazed plots (n = 78)	Grazed plots (n = 50)
Ramets (No.)	13.31 ± 11.31	11.23 ± 10.16	16.56 ± 12.31
Fertile fronds (No.)	6.04 ± 9.36	7.55 ± 10.87	3.68 ± 5.64
Sterile fronds (No.)	44.09 ± 40.08	38.7 ± .34.92	52.48 ± 47.74
Total frond area (m²)	7.57 ± 9.31	8.42 ± 10.45	6.23 ± 7.05
Mean height (cm)	70.14 ± 48.67	79.86 ± 55.91	54.96 ± 28.90

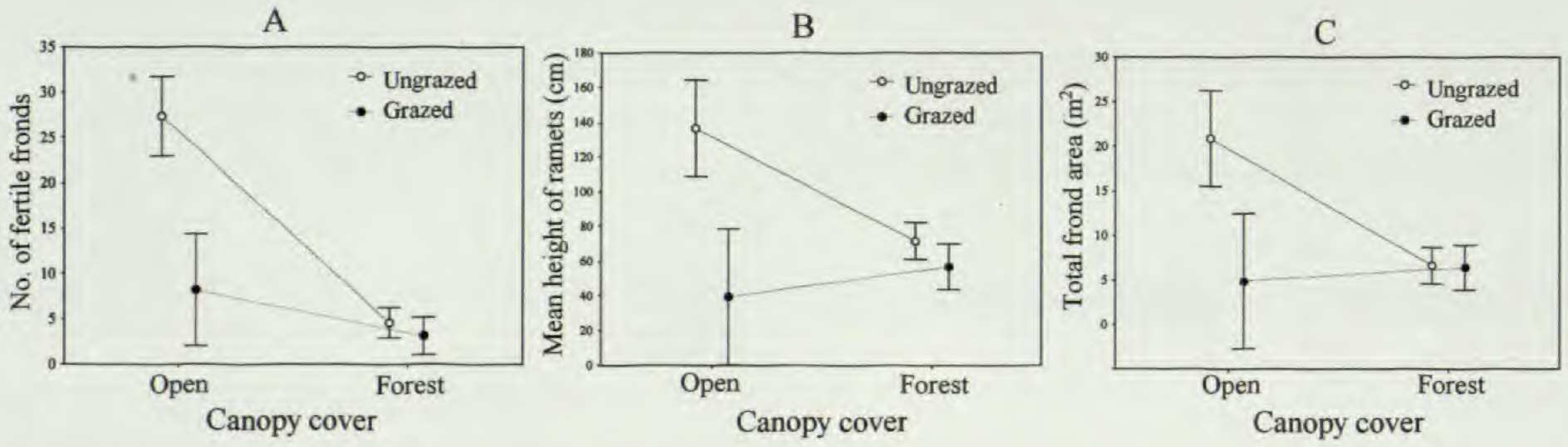

FIG. 5. Effects of grazing (grazed and ungrazed) and canopy cover (open and forest) on the number of fertile fronds (A), mean height (B) and total frond area (C). Means (dots) and 95% confidence intervals (vertical bars) are shown. The interactions were significant at 0.01 level (two-way ANOVA).

area ($F_{1,124}$ = 10.09; $P < 0.01$). The effect of grazing on these frond traits was greater in open than in forest plots (Fig. 5). Grazing and the interaction between canopy cover and grazing were found to have no significant effect on the number of sterile fronds and number of ramets.

DISCUSSION

The results showed that the number of fertile fronds increased with the number of sterile fronds. However, the variation in the number of fertile fronds between ramets with different numbers of sterile fronds underlines that the production of fertile fronds also depends on other factors (e.g., light and nutrients) favoring their development.

The stronger correlation between the number of fertile fronds and the mean height of ramets suggests that fertile fronds are higher than sterile fronds. The parameter of height can be related or unrelated to light and frond density in different species of ferns (see Hill and Silander, 2001). We observed that light appears to promote fertility in *O. regalis*, as the number of fertile fronds increased considerably with greater height, while these two positively correlated characteristics decreased with forest canopy cover. The analysis of total frond area and canopy cover revealed that fronds are fewer and smaller in plots under high tree cover. Odland *et al.* (2006) indicated similar results in the dimorphic fern *Matteuccia struthiopteris*. Thus, *O. regalis* performs best in conditions of full sunlight but can persist and recruit young sporophytes under a very dense tree canopy.

Until the early 1900s this fern was reported in many locations in central Italy, prevalently in marsh and lake environments. After 1950 these environments underwent considerable land use changes for both intensive farming and industry, due to the increasing human population (Falcucci *et al.*, 2007). These changes led to the extinction of many *O. regalis* populations and the remaining populations are mainly located in streams and springs within forests. For these reasons we collected much more data under high tree cover than in open habitats. Within forests, the sunny habitats preferred by *O. regalis* may be found in both human-altered environments (alongside paths) and in natural gaps (i.e., spring swamps) (Landi and Angiolini, 2008). However, as moist and open habitats are appropriate sites for the growth and production of fertile fronds, conservation efforts should focus primarily on the maintenance of marshes in open habitats and spring swamps in forest habitats.

On the Isle of Rum, Wood (2000) notes that *O. regalis* is very sensitive to grazing and is present in the few places that are inaccessible to deer, while it is a common component of the vegetation on other ungrazed islands nearby. In Tuscany, deer have been observed grazing *O. regalis* fronds and bark stripping has been detected on the trees in the surrounding vegetation that is more susceptible to this damage (i.e., *Alnus glutinosa, Frangula alnus, Populus tremula, Carpinus, Fraxinus* and *Quercus*) (see Gill, 1992).

The results presented here show that the number of fertile fronds, the mean height of ramets and total frond area is significantly lower in grazed plots than in ungrazed plots. The interaction between grazing and canopy cover indicates that grazing affects more open than forest sites. The number of ramets and sterile fronds were unaffected by grazing. Moreover, the number of ramets was higher in grazed plots than ungrazed plots. This may be related to the higher abundance of ramets in open areas (i.e., spring swamps, see Landi and Angiolini, 2008), which are more affected by grazing.

Our data suggest that fertile and sterile fronds of *O. regalis* respond differently to the availability of light and to grazing. These results can be used to formulate the following alternative explanations: i) deer prefer fertile fronds; ii) ramets with damaged fronds become weakened and produce fewer fertile fronds after grazing by deer. Ferns can be a valuable source of food for deer in winter, before leaves have appeared on woody vegetation (Healy, 1971). However, this cannot be the case with *O. regalis* as it is a deciduous herbaceous fern with fronds that develop in May and become senescent in September. Thus, this fern can only be grazed in summer, when food is fully available in the surrounding vegetation.

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